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Plant Signalling: The opportunities and dangers of chemical communication

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Running head: Plant signalling

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Abstract

The notion of chemical communication between plants and other organisms has gone from being viewed as a fringe idea to an accepted ecological phenomenon only recently. An Organized Oral Session at the August 2010 Ecological Society of America meeting in Pittsburgh examined the role of plant signalling both within and between plants, with speakers addressing the remarkably wide array of effects that plant signals have on plant physiology, species interactions, and entire communities. In addition to the familiar way that plants communicate with mutualists like pollinators and fruit dispersers through both chemical and visual cues, speakers at this session described how plants communicate with themselves, with each other, with herbivores, and with predators of those herbivores. These plant signals create a complex odor web superimposed upon the more classical food web itself, with its own dynamics in the face of exotic species and rapid community assembly and disassembly.

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1 Introduction

The notion of chemical communication between plants and other organisms has gone from being viewed as a fringe idea to an accepted ecological phenomenon only recently. Within the past two years, the number of published examples of this phenomenon has more than doubled. An Organized Oral Session at the August 2010 Ecological Society of America meeting in Pittsburgh examined the role of plant signalling both within and between plants. Speakers addressed the remarkably wide array of effects that plant signals have on plant physiology, species interactions, and entire communities.

In addition to the familiar way that plants communicate with mutualists such as pollinators and fruit dispersers through both chemical and visual cues, speakers at this session described how plants communicate with themselves, with each other, with herbivores, and with predators of those herbivores. As on the Internet, once information is broadcast, even if only among "friends," it becomes available for other unintended and unexpected uses. The hand of natural selection then works in unexpected ways to alter the character, timing and interpretation of signals.

2 Private signals versus public information

Some communication acts as a form of coordination among actors with common interests, such as different parts of the same plant, neighboring but possibly related plants, or plants and the predators or parasites that attack herbivores. This communication, which presumably evolved to hinder herbivores or pathogens, can be hijacked or subverted in many ways. The signalling cascades familiar in cell biology are designed for coordination of responses within an individual, and hardly seem like public information. Nonetheless, Gitta Coaker (University of California at Davis) showed how pathogens like *Pseudomonas* *syringea* have found ways to interfere with these internal signalling cascades. In another twist, the effector molecules that bacteria inject into cells in order to subvert plant defenses are themselves part of the signal that plants use to recognize bacteria in the first place. Rick Karban (University of California at Davis) discussed how volatile chemicals can be used for within-plant communication and often have advantages as within-plant signals compared to vascular signals. By broadcasting that information more publicly, it becomes available to neighbors who have been shown to use cues to defend themselves and reduce damage.

These talks raise issues about the basic nature of signalling interactions and the effects of signals on receiving individuals. Low levels of a potential toxin act as effective signals of danger, just as bacterial effector molecules serve as compelling evidence of attack. Ray Callaway (University of Montana) showed how invasive plants create signals, toxins or both that have much larger negative effects on evolutionarily naive neighbors in their non-native than on neighbors that share some evolutionary history in their native range.

3 Context is everything

Politicians have taught us that their words must be taken in context. The same is true of communication involving plants. Although sometimes maddening to ecologists, a chemical that means one thing in one context might mean something else in another. Katja Poveda (Georg August Universität, with Andre Kessler of Cornell University) showed that plant defenses may interfere with the well-established benefits of signalling to pollinators, and that plants that have been attacked produce chemicals that secondarily deter pollinators and reduce seed set. Whether the pollinators somehow use this as a cue to avoid less favorable plants or the defenses act directly against the pollinators remains unknown.

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This is just one way in which plant signals find themselves involved in a web of interactions, the odor web superimposed upon the food web. This web involves multiple signals, multiple signalers, and multiple signal recipients. Ezra Schwartzberg (Penn State University) showed how aphids subvert plant defenses through inhibiting the release of volatile organic compounds that attract predators, apparently by directly eliminating the key signalling molecule jasmonic acid. If beet armyworm caterpillars colonize a plant after it has been attacked by aphids, they too can escape the plant volatile compounds, and potentially experience greater fitness. Marcel Dicke (Wageningen University) boldly stated that nothing in biology makes sense except in the light of body odor. As in the work by Schwartzberg, he showed how communities of insects on plants are affected by the order of arrival, because this shapes the body odor web upon which the food web itself is formed. Those herbivores that suppress signals can attract others, leading to a high-dimensional and unpredictable environment for which organisms may or may not be matched.

Pathogens can manipulate the odor web to enhance their transmission. Mark Mescher (Penn State University) showed how cucumber mosaic virus makes its host plant more attractive but of lower quality to the aphids that transmit it, thus promoting the spread of this acute infection. In contrast, the bacterial pathogen *Erwinia tracheiphila* attracts cucumber beetles to the wilting leaves it attacks, and those beetles are subsequently attracted to the flowers of uninfected plants.

Even the most compelling speech would fall flat if people did not speak the language. As seen in the work of Callaway and Dicke, matches and mismatches between signalers and signal receivers shape the ecological consequences of the odor web. Colin Orians (Tufts University) showed that the performance of exotics can be enhanced by mismatches at

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higher trophic levels. The non-native willow *Salix dasyclados* is both more resistant to Swedish herbivores and produces volatiles that make it equally attractive to predators as the native willow *Salix cinerea*. Chris Frost (Penn State University) presented evidence that plants can use volatile signals from nearby damaged leaves to place themselves on alert for a more rapid response to actual damage, and that these "priming" responses can depend sensitively on the details of the volatile bouquet. Interestingly, *Populus* can be primed both by its own volatiles and those from the surely evolutionarily unfamiliar maize.

4 Evolution of signals

A striking element of many signalling webs, and indeed of regulatory systems in general, is the existence of a relatively small number of points of vulnerability. Jasmonic acid emerges as just such a point within the plant, as shown in the work of Ezra Schwartzberg on aphid subversion and Chris Frost on priming. Within the plant, Gitta Coaker showed how the protein RIN4 plays a pivotal role, becoming a target for bacterial interference.

These points of vulnerability within individual plants contrast with the multiplicity of signalling modalities that reach the open air. Maurice Sabelis (University of Amsterdam) demonstrated the evolutionary consequences of how signals are susceptible to subversion, stealth or simple deceit. Given the choice, any signal receiver with even slightly different interests from the signaler should pay attention only to signals that convey "honest" information. But these honest signals, like those from plants to predators that attack plant herbivores, can be subverted by plants that "cry wolf" and signal for help when they have not yet been attacked. These signals will be increasingly ignored by predators, only to replaced by new informative signals, leading to unstable dynamics and the proliferation

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of signals over time.

Rick Karban concluded the session by examining what we know about the fitness consequences of the many varieties of plant signalling. Signalling to mutualists like pollinators does indeed increase plant fitness, while signals that unintentionally attract herbivores reduce fitness. There is as yet little known about the fitness effects of attracting predators, nor even of the fitness effects of many signals within plants that work to reduce damage. Signals to neighbors have been shown to reduce damage and increase components of fitness in a couple of systems. However, given the complexity and context-dependence of every signalling web, we might expect these fitness effects to vary substantially in time and space, not least due to the evolutionary dynamics described by Sabelis.

Ultimately, one can ask whether odor webs are any more organized or evolved than food webs themselves. Communities range from the seemingly tightly coevolved to the recently assembled, functioning somehow in the face of novel interactions and novel cues. Exotic species, and the signalling mismatches they create, might give us some of the best natural experiments to understand how this invisible web works. However the species were assembled, signals play a crucial role in how plants avoid damage and find mates, and how their herbivores and predators find food and avoid attack.